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Insect-Like Olfactory Adaptations in the Terrestrial Giant Robber Crab

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Summary

The robber crab (*Birgus latro*), also known as the coconut crab, is the world's largest land-living arthropod, with a weight reaching 4 kg and a length of over half a meter [1]. Apart from the marine larval stage [2, 3], this crab is fully terrestrial, and will actually drown if submerged in water [4]. A transition from sea to land raises dramatically new demands on the sensory equipment of an animal. In olfaction, the stimulus changes from hydrophilic molecules in aqueous solution to mainly hydrophobic in the gaseous phase [5]. The olfactory system of land crabs thus represents an excellent opportunity for investigating the effects of the transition from sea to land. Have land crabs come to the same solutions as other terrestrial animals, or is their olfactory sense characterized by unique innovations? Here, we show that the robber crab has evolved an olfactory sense with a high degree of resemblance to the insect system. The similarities extend to physiological, behavioral, and morphological characters. The insect nose of the robber crab is a striking example of convergent evolution and nicely illustrates how similar selection pressures result in similar adaptation

Results and Discussion

Crabs Display Odor-Guided Behavior

Robber crabs can be found on islands from the Indian Ocean to the central Pacific. However, extensive hunting and habitat exploitation during the past 100 years have drastically diminished the distribution range of this formerly widespread species [6, 7]. These crabs have long fascinated sailors and explorers of the Indo-Pacific region (e.g., [8–10]), and although many of their tales are somewhat exaggerated (Figure 1A), the key elements of the stories are true. The robber crabs are certainly capable of climbing tall trunks in search of fruits (Figure 1B). Coconuts can indeed be peeled and cracked open, although they are only eaten if other more quickly handled resources are not available because the opening process takes several weeks [6]. The robber crabs can best be described as opportunistic scavengers, although their massive size, aggressiveness, and huge claws also make them formidable predators [6, 11] (Figure 1C). It is assumed that these mainly nocturnal animals use olfaction to locate food [1, 6] because other terrestrial crabs have been shown to respond behaviorally to odors [12–14]. According to Christmas Island inhabitants, robber crabs are highly inquisitive and will rapidly find and frequently also steal any unattended, smelly objects. First we aimed to confirm this reputed long-distance attraction to odors. We distributed baits (Figure 1D), containing favored resources: dead red crabs (*Gecarcoidea natalis*), coconut flesh, and pith of the *Arenga* palm, as well as empty control baits. Baits were placed in groups of four (three of each bait type plus control) at three locations and were then examined every half hour after sunset. The baited observation posts were almost immediately (within minutes) located by robber crabs and were subsequently visited by high numbers, when considering the density of the population in the area (roughly 100 crabs per hectare [6]). After 4.5 hr of observation, we recorded a total of 14 visits to the red crab baits, 8 to the coconuts, and 4 to the *Arenga*. The empty control baits on the other hand were not visited at all during the observation period. Thus, the reputed capacity of the robbers to locate objects by odor holds true.

Odors Are Detected by the Terminal Segment of the Antennule

How are odors detected by the robber crab? The olfactory organs in most examined crustaceans have been shown to be the aesthetascs on the antennules [15, 16]. In the robber crab, which has prominent antennules, these each comprise three basal segments and a pair of flagella and look superficially very similar to those of terrestrial hermit crabs [17] (Figure 2A). Although functional evidence of a role of the antennules as olfactory organs is lacking in hermit crabs, the ultrastructure strongly suggests an olfactory function. Are the antennules olfactory organs in the robber crab?

To address this question, we utilized electroantennographic (EAG) detection, which, as used here, is a technique in which the recording output represents the summed activity of a large proportion of the olfactory receptor neurons [18]. The EAG technique has been routinely applied to the insect system but has never, to our knowledge, been successfully used in any crusta-

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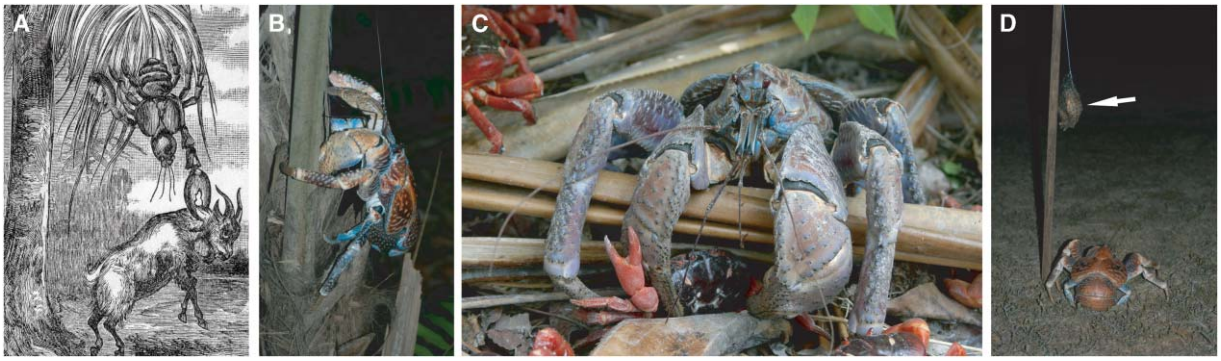

Figure 1. A Monstrous Crab

(A) The robber crab (*Birgus latro*) is the largest land-living arthropod. Their peculiar habits and looks have given rise to numerous myths and legends. Although exaggerated, this illustration from the 19th century does contain some truths.

(B) Robber crabs are extraordinarily strong and excellent climbers. They are capable of climbing tall palm trees in search of fruits and coconuts, the latter of which the crabs can peel and crack using their huge claws.

(C) Robber crabs are scavengers and mostly nocturnal. However, their strength, agility, and aggressiveness also make them fearsome predators.

(D) Wooden poles with baits attached (arrow), containing dead red crabs, coconut, or *Arenga* were placed along transects in suitable robber crab habitats. Crab activity around the baits was subsequently monitored after sunset. These simple experiments demonstrate that the robber crabs display odor-guided behavior.

cean. Initial robber crab EAG recordings, using the volatile-odor headspace of the bait types mentioned above as stimuli, produced distinct EAG responses from the flagellum (Figure 2B), whereas the basal segments of the antennules and the first antennae did not show any activity in response to the stimuli. The presence of chemoreceptors located elsewhere, e.g., on legs or chelae, was not investigated, due to experimental and permission restrictions, and can hence not be excluded.

The Robber Crab Has a Sensitive and Selective Olfactory System

Having concluded that EAG recordings in the robber crab are feasible and that the antennules indeed operate as olfactory tissue, we continued to investigate the properties of the system in more detail. First, we found that the antennules were sensitive to CO_2. Responses were clearly dose dependent (Figure 2C) and characterized by a rapid depolarization followed by a less-prominent and slower hyperpolarization (Figure 2D). The characteristics of the CO_2 response in the robber crab are similar to those of insects, for which CO_2 detection appears to be critically important (e.g., [19, 20]). The potent CO_2 receptors have probably evolved as an adaptation to terrestrial conditions and are likely of importance for resource localization (e.g., cadavers—a favorite dish—release large quantities of CO_2 as a result of the microbial degradation activity) and for monitoring CO_2 levels in burrows. We also found that the antennules responded to water vapor, which contrary to CO_2, elicited a positive EAG response (Figure 2E). Interestingly, positive EAGs elicited by water have also been frequently observed in insect systems.

Next, we proceeded to test a number of synthetic odor stimuli. The selected odorants, representing various food sources and chemical classes, were the carcass odors dimethyltrisulfide (DMTS) and dimethyldisulfide (DMDS), pineapple odor (ethyl hexanoate), flowery odor (phenylacetaldehyde), the coconut odors γ-nonalactone and delta-decalactone, and banana odor (isoamyl acetate). The olfactory system of the crabs was clearly able to detect all these compounds but to very different degrees (Figures 2F and 2G). The response pattern shows an impressive overall selectivity and sensitivity of the system (Figure 2H). Compounds of structural proximity were clearly separated, indicated by the shapes of the dose response curves, and the odorants, in particular DMTS, triggered responses at very low doses. The sensitivity to DMTS (responding already at 0.1 ng stimulus load) is in line with the notoriously sensitive insect pheromone receptors [21] and with the most-sensitive insect plant-odor receptors recorded [22]. Considering the importance of carrion as a food source for the crabs, the high sensitivity to DMTS is understandable. However, γ-nonalactone, which to the human nose smells most characteristically of coconut, turned out to be a weak ligand, requiring fairly high doses to elicit activity. If odors are used at all by the crabs to locate coconuts, they likely rely on other compounds. As coconuts are visually conspicuous, it is conceivable that coconuts are initially located through visual cues rather than olfactory. However, once the coconuts have been peeled and cracked, olfactory cues may be more important than visual cues because the coconuts are not left out in the open but rather are hidden by the individual in possession of this precious resource.

Robber Crab EAGs Are Indistinguishable from Insect EAGs

The EAG activity elicited in response to stimulation with CO_2, water, and odorants shows strong similarities with that demonstrated in insects. The responses are characteristically dose dependent and display the typical dynamics of insect EAGs. We performed a more-detailed analysis of the kinetic profile of the EAG responses (Figure 3A). We divided the EAGs into four discrete phases:

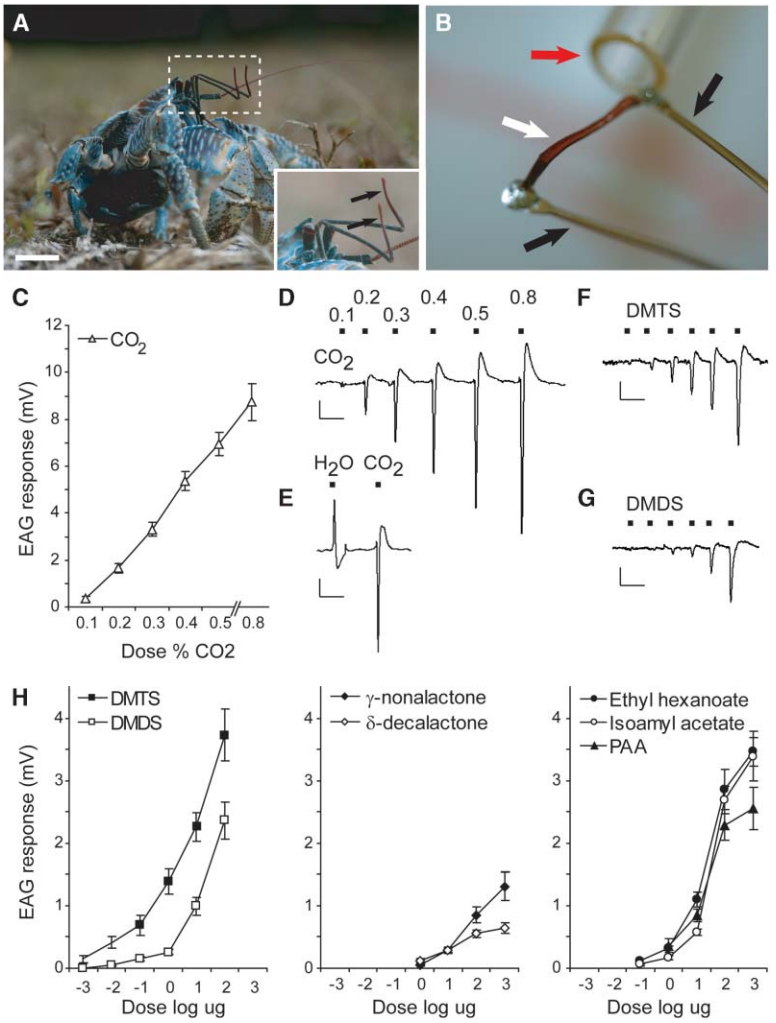

Figure 2. Robber Crab Olfactory Physiology

(A) Olfactory detection is accomplished by the terminal segment of the antennules, the flagellum (marked by black arrows in the insert of the boxed area). The scale bar represents 5 cm.

(B) A flagellum (white arrow) mounted between two electrodes (black arrows) for electroantennographic (EAG) detection. A red arrow marks the outlet passing the constant airflow over the preparation.

(C and D) EAG recordings reveal CO_2 as a potent ligand, eliciting responses in a dose-dependent manner.

(E) The antennules are also sensitive to water, however, which elicits inverted, positive EAGs.

(F and G) EAGs for dimethyl trisulfide (DMTS) (F) and dimethyl disulfide (DMDS) (G) presented in increasing dosages (decadic steps from 1 ng to 100 μg). The two compounds, although of structural proximity, have distinctively different activity patterns.

(H) Plotted dose response functions for the screened compounds. The horizontal scale bars represent 10 s, and the vertical scale bars represent 1 mV.

(I) initial rapid depolarization, (II) return to baseline, (III) hyperpolarization, followed by (IV), an outdrawn return to baseline. We measured the time for each event and then compared the time profile of the crab EAGs with that of EAGs recorded from an insect (exemplified by the fruitfly, *Drosophila melanogaster*). The analysis revealed that the EAGs from the crab are not only similar but are actually identical to insect EAGs (Figure 3B). The EAG profiles are moreover independent of the odor stimulus identity (Figure 3C). Furthermore, the rapidity of the crab's EAG responses implies a swift and efficient transduction pathway, well able to cope with terrestrial conditions.

Robber Crab Behavior Toward Single Odor Compounds

Do the crabs also respond behaviorally to these odors? Using the same behavioral assay as described previously, we tested the effect of DMTS. Six groups of two baits (each group with one DMTS and one control bait) were placed along a ca. 1 km transect through the rainforest. The baited poles were rapidly found and visited in high numbers. After 4 hr of observation, each DMTS bait had been visited by 6.2 $\pm$ 1.11 ($\pm$SEM) crabs, whereas the control traps only had 0.2 $\pm$ 0.2 visitors (significantly different, paired t test $p < 0.01$). The crabs were observed to detect the odor source from a distance (>50 min). Detection typically triggered an upwind search for the source, with the crabs constantly sampling the air by flicking their antennules. This behavior is very similar to that of aquatic crustaceans, in which the flicking is supposed to be a stimulus acquisition adaptation to a viscous environment [23, 24]. However, the flicking probably also increases olfactory performance in the air because insects frequently also flick their antennae when they come into contact with an odor plume. Apart from DMTS, we also tested γ-nonalactone. In line with the physiological results, this compound elicited no behavioral response (zero visits in total). Thus, the crabs do not respond indiscriminately to any smelly objects they encounter but rather show a selective preference for specific odorants. The behavioral response to DMTS shows strong similarities to that of carrion-attracted insects. In particular, blowflies find DMTS irresistible [25] and show a comparably high sensitivity toward this compound. It is interesting that DMTS appears to have evolved as a ubiquitous signal of decaying meat in both robber crabs and carrion insects.

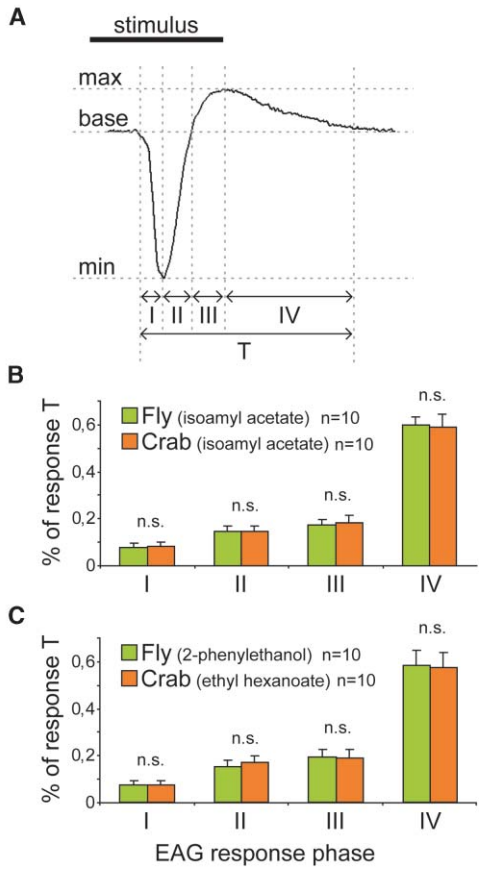

Figure 3. Electroantennogram Response Kinetics

(A) The EAG responses can be broken up into four distinct phases: (I) initial rapid depolarization, (II) return to baseline, (III) hyperpolarization, followed by (IV), an outdrawn return to baseline.

(B) Comparing the EAG kinetics from the robber crab with EAG kinetics from an insect (exemplified here by a fruitfly, *D. melanogaster*) shows that the EAG profiles (in response to isoamyl acetate at 1 μg) are indistinguishable from each other (no significant difference [n.s.], paired t test [$p > 0.1$]).

(C) The similarities in EAG profile extend to other odorants as well. The EAG responses to ethyl hexanoate (1 μg) from the crab and the responses to 2-phenylethanol (1 μg) from the fly are also indistinguishable.

The Robber Crab Aesthetascs Share Key Principles with Insect Olfactory Sensilla

How is the olfactory system configured? Overall, the organization of the peripheral components of the olfactory system in the robber crab is strikingly different from that of aquatic crustaceans and closely follows that of its smaller, land hermit crab relative *Coenobita compressus* [17]. The aesthetascs of the robber crab are confined to the ventral side of the primary flagella and are arranged in ordered rows along a central groove. The aesthetascs are short and blunt (Figures 4A and 4B) and hence externally more similar to insect olfactory sensilla than to the long and slender aesthetascs found among marine crustaceans [18]. Furthermore, the robber crab aesthetascs have an asymmetric profile; the protected side of the aesthetascs is lined with a thick cuticle, whereas the exposed side is covered with a thinner cuticle, which shows a concave wrinkly surface through which the odorants are presumably able to pass [18] (Figures 4B and 4H). This feature is markedly different from that of marine crustaceans, which show symmetric aesthetascs and primarily the thin type of cuticle [26]. Further distinguishing the robber crab aesthetascs from those of virtually all marine crustaceans (an exception being the brackish-water living *Monoporeia affinis*) is the organization of the basal bodies and cilia segments [17, 26] (Figure 4C). In the robber crab, the basal bodies and cilia segments are housed well inside the flagellum (Figure 4F) and are surrounded by a lymph space, an organization that closely follows that of insect sensilla. Marine crustaceans, on the other hand, lack the internal lymph space and have basal bodies and cilia segments housed in the aesthetasc hair, i.e., located outside the flagellum [17]. Aesthetascs of the robber crab house a large number of neurons ($\sim$30–50), an organization that is closer to that found in other crustaceans (e.g., [26]) than to what is typically found in insects (2–4 neurons; e.g., [27]). However, similar to the robber crab and other crustaceans, some insects, such as Hymenopterans (e.g., bees) and Orthopterans (e.g., locusts), have olfactory sensilla housing large numbers of neurons [28]. The homologies between the robber crab (and its land hermit crab relative) and insects are likely to be convergent adaptations to terrestrial conditions and have presumably arisen in both groups as a mechanism to minimize water evaporation and to give increased protection from a hostile terrestrial environment. Thus, the robber crab aesthetascs display a mosaic of characteristics that show similarities to insect sensilla as well as to the general crustacean organization, the latter being a natural consequence of the ancestry.

In this study, we have addressed the question of how the robber crab has solved odor detection in its terrestrial environment. We show that they have evolved an olfactory system that is not only fully functional on land but is also highly efficient, a feat that to a large extent has been achieved through adopting solutions similar to those of their arthropod relatives, the insects. In summary, the robber crab olfactory system is a notable example of how similar needs result in convergent adaptations.

Experimental Procedures

Animals

All experiments were carried out on Christmas Island, Australia (105°40′E, 10°35′S), with permission to collect, handle, and experiment with the crabs granted by Parks Australia North. All experiments were carried out with methods that were as noninvasive as possible, and no animals were killed during any of the experiments.

Electrophysiology

Electroantennogram (EAG) recordings were performed by mounting an excised antennal flagellum between two recording electrodes. The electrodes were placed at opposite ends of the excised flagella and the connectivity enhanced by the use of electrogel. The recording electrodes were connected to a preamplification probe, in turn connected to a custom-made, field-modified Syntech amplifier/IDAC converter (Syntech, Hilversum, The Netherlands). The EAG recordings were performed indoors, at the field station of the Christmas Island National Park. The signal recorded in this fashion is believed to represent the summed activity of the olfactory receptor neurons. The signal was DC filtered, amplified (1000×), stored on

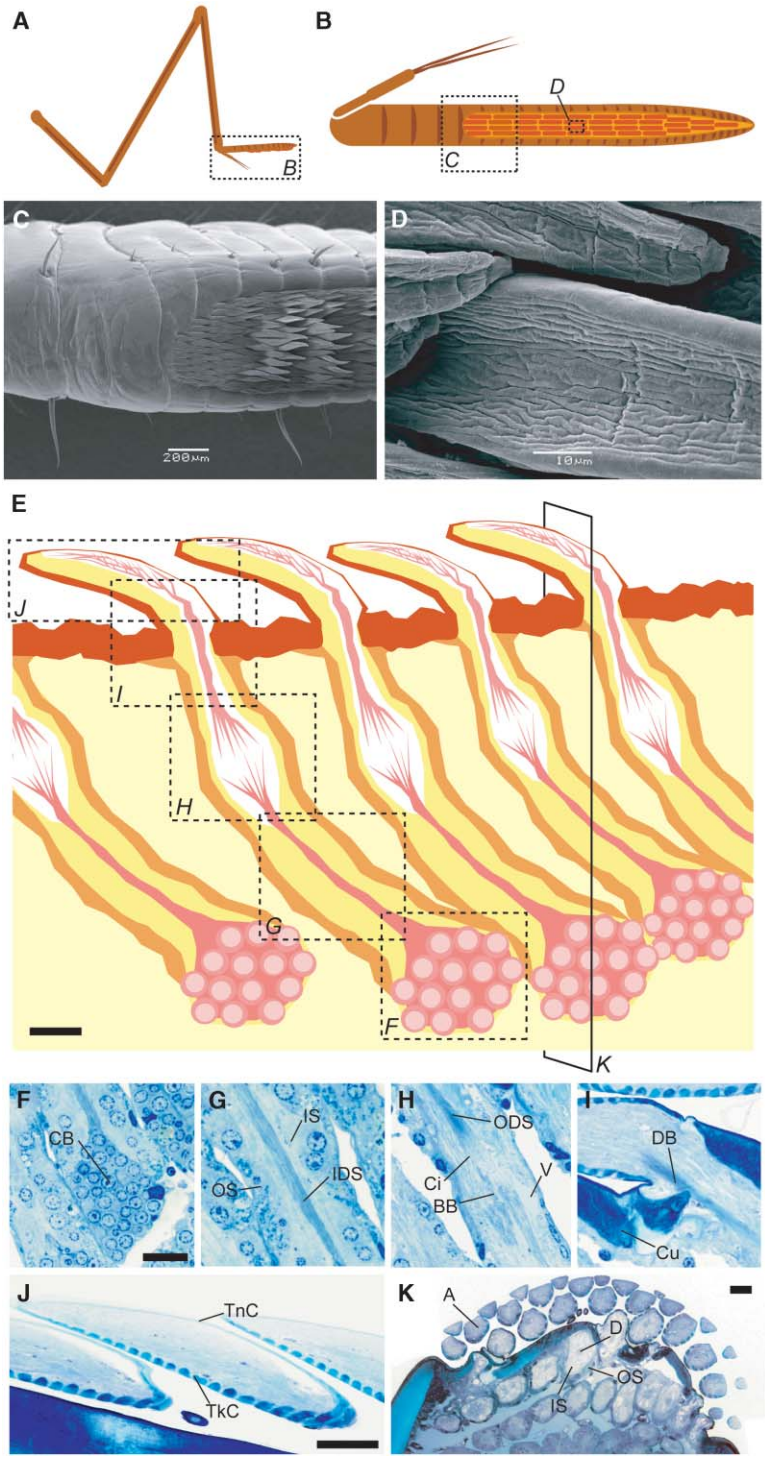

Figure 4. Aesthetasc Structure and Organization

(A) Schematic drawing of the antennule (side-view). Boxed area, which indicates the flagellum, is shown in (B).

(B) Schematic drawing of the ventral side of the flagellum. The approximate locations of the SEM images (C and D) are indicated by the boxed areas.

(C) SEM image showing the ventral side of the flagellum with the aesthetascs arranged in neat rows.

(D) Close-up view of the aesthetascs, showing their asymmetric profile. The exposed side has a concave, wrinkled surface, whereas the protected side is smooth.

(E) Schematic drawing of the aesthetasc organization as seen through a longitudal section. Boxed areas are represented in the corresponding, subsequent panels.

(F) The sensory cell bodies (CB) give rise to the inner dendritic segment (IDS).

(G) The IDS is protected by an inner and an outer cell sheath (IS and OS, respectively).

(H) Surrounded by a receptor lymph space (V), the dendrites fan out and form basal bodies (BB) that give rise to cilia (Ci), which recollect and form the outer dendritic segment (ODS).

(I) The dendritic branches (DB) entering the aesthetasc hair, protruding from the flagellar cuticle (Cu).

(J) The exposed side of the aesthetascs is covered by a thin, presumably permeable cuticle (TnC), whereas the protected side is lined with a thick cuticle (TkC).

(K) Transverse section through the flagellum. The asymmetrical profile of the aesthetascs (A) can be seen, as well as the distinction between the IS, OS, and dendrite (D). The scale bars in Figures (C)–(I) represent 25 μm.

a PC laptop, and analyzed with the EAG2000 software (Syntech). In total, the response profiles of ten flagella, collected from ten different animals (five males and five females of varying size and from unknown molting stages), were examined. All the tested odorants were obtained from Sigma-Aldrich and were of >98% purity and diluted in paraffin oil in decadic steps from 100 pg/μl to 10 μg/μl. Ten microliters of the compound at the test concentration was pipetted onto a small piece (~1 cm^2) of filter paper, which was subsequently placed inside a plastic 1 ml syringe. The air volume inside the syringe containing the volatile odor substance was then ejected (by compressing the syringe, generating an estimated ~0.5 s air pulse) into a humidified, constant air stream (sustained by an aquarium pump, flowing at 0.5 m/s) passing over the excised flagellum. Control stimulations were performed in the same manner but with syringes only containing the solvent. EAG recordings from fruitflies (*D. melanogaster*, Oregon-R) were performed on whole mounted antennae, with a stationary Syntech EAG set up controlled by the same EAG2000 software and following the same procedure as outlined above.

Behavior

The behavioral experiments were carried out on the Central Plateau (vicinity of the National Park research station) and by the North-

West Point (along the Dale). Baits were made from plastic mesh bags tied to wooden poles at 0.5 m above ground (to prevent the crabs from reaching the baits and obtaining tactile and taste cues). The baits were placed in groups, each group contained experiment and control baits, spaced ca. 10 m apart and each group separated by at least 200 m. Experiments were carried out after sunset, to prevent the crabs from relying on visual cues. Crab activity was monitored every 30 min (through use of flashlights), and crabs were scored as visiting a bait if found present within a 1 m radius of the bait. Trials with synthetic odorants (DMTS and γ-nonalactone) were performed with the compounds diluted 1:3 in paraffin oil. Open 2 ml plastic vials with 500 μl of the odorant solutions were placed inside the mesh bags. The control baits contained vials with only paraffin oil.

Morphology

Antennules from 12 crabs were collected and preserved in 70% ethanol. Two antennules were sectioned and analyzed under a light microscope (Olympus AX70 mounted with a DP70 camera). Three samples were examined in a scanning electron microscope (SEM) (JEOL JSM T 330). Preparation and mounting of the tissue for SEM followed standard procedures (as in [15]).

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References

1. Greenaway, P. (2003). Terrestrial adaptations in the anomura (Crustacea: decapoda). Mem. Mus. Vic. *60*, 13–26.
2. Reese, E.S. (1968). Shell use: An adaptation for emigration from the sea by the coconut crab. Science *161*, 385–386.
3. Reese, E.S., and Kinzie, R.A. (1968). The larval development of the coconut or robber crab *Birgus latro* (L.) in the laboratory (Anomura, Paguridae). Crustaceana, Suppl. *2*, 117–144.
4. Brown, I.W., and Fielder, D.R. (1991). The coconut crab: Aspects of *Birgus latro* biology and ecology in Vanuatu. (Canberra: Australian centre for International Agricultural Research).
5. Freitag, J., Ludwig, G., Andreini, I., Rössler, P., and Breer, H. (1998). Olfactory receptors in aquatic and terrestrial vertebrates. J. Comp. Physiol. [A] *183*, 635–650.
6. Hicks, J., Rumpff, H., and Yorkston, H. (1990). Christmas crabs, 2nd edition. (Christmas Island Natural History Association, Christmas Island).
7. Lavery, S., Mortiz, C., and Fielder, D.R. (1996). Indo-Pacific population structure and evolutionary history of the coconut crab *Birgus latro*. Mol. Ecol. *5*, 557–570.
8. Drake, Sir Francis. (1628). The world encompassed by sir Francis Drake, being his next voyage to that to Nombre de Dios; collected out of the notes of F. Fletcher and others. (London: Nicholas Bovrne).
9. Rumphius, G.E. (1705). D'Amboinsche Rariteitkammer. (Amsterdam).
10. Darwin, C. (1845). Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of H.M.S. Beagle Round the World: Under the Command of Capt. Fitz Roy. (London: John Murray).
11. Helfman, G.S. (1977). Agonistic behaviour of the coconut crab, *Birgus latro* (L.). Z. Tierpsychol. *43*, 425–438.
12. Rittschof, D., and Sutherland, J.P. (1986). Field studies on chemically mediated behavior in land hermit crabs (*Coenobita rugosus*): Volatile and non-volatile odors. J. Chem. Ecol. *12*, 1273–1284.
13. Wellins, C.A., Rittschof, D., and Wachowiak, M. (1989). Location of volatile odor sources by ghost crab *Ocypode quadrata* (Fabricius). J. Chem. Ecol. *15*, 1161–1169.
14. Small, M.P., and Thacker, R.W. (1994). Land hermit crabs use odors of dead conspecifics to locate shells. J. Exp. Mar. Biol. Ecol. *182*, 169–182.
15. Ache, B.W., and Derby, C.D. (1985). Functional organization of olfaction in crustaceans. Trends Neurosci. *8*, 356–360.
16. Derby, C.D., and Atema, J. (1998). Chemoreceptor cells in aquatic invertebrates: Peripheral mechanisms of chemical signal processing in decapod crustaceans. In: Sensory Biology of Aquatic Animals (Atema, J., Fay, R.R., Popper, A.N., and Tavolga, W.N. eds.) (Berlin: Springer-Verlag).
17. Ghiradella, H., Case, J., and Cronshaw, J. (1968). Fine structure of the aesthetasc hairs of *Coenobita compressus* Edwards. J. Morphol. *124*, 361–386.
18. Schneider, D.Z. (1957). Elektrophysiologische untersuchungen von chemo- und mechanorezeptoren der antenne des seidenspinners *Bombyx mori*. Z. Vergl. Physiol. *40*, 8–41.
19. Dekker, T., Takken, W., and Braks, M.A. (2001). Innate preference for host-odour blends modulates degree of antropohagy of *Anopheles gambiae* sensu lato (Diptera: Culicidae). J. Med. Entomol. *38*, 868–871.
20. Thom, C., Guerenstein, P., Mechaber, W., and And Hildebrand, J.G. (2004). Floral CO_2 reveals flower profitability to moths. J. Chem. Ecol. *30*, 1285–1288.
21. Kaissling, K.-E., and Priesner, E. (1970). Die Riechschwelle des Seidenspinners. Naturwissenschaften *57*, 23–28.
22. Hansson, B.S., Larsson, M.L., and Leal, W.S. (1999). Green leaf volatile detecting olfactory receptor neurones display very high sensitivity and specificity in a scarab beetle. Physiol. Entomol. *24*, 121–126.
23. Schmidt, B.C., and Ache, B.W. (1979). Olfaction: Responses of a decapod crustacean are enhanced by flicking. Science *205*, 204–206.
24. Koehl, M., Koseff, J., Crimaldi, J., MacKay, M., Cooper, T., Wiley, M., and Moore, P. (2001). Lobster sniffing: Antennule design and hydrodynamic filtering of information in an odor plume. Science *294*, 1948–1951.
25. Stensmyr, M.C., Urru, I., Collu, I., Celander, M., Angioy, A.M., and Hansson, B.S. (2002). Rotting smell of dead-horse arum florets. Nature *420*, 625–626.
26. Hallberg, E., Johansson, K.U., and Elofsson, R. (1992). The aesthetasc concept: Structural variations of putative olfactory receptor complexes in Crustacea. Microsc. Res. Tech. *22*, 325–335.
27. Shanbhag, S., Müller, B., and Steinbrecht, A. (1999). Atlas of olfactory organs of *Drosophila melanogaster* 1. Types, external organization, innervation and distribution of olfactory sensilla. Int. J. Insect Morphol. & Embryol. *28,* 377–397.
28. Schneider, D., and Steinbrecht, R.A. (1968). Checklist of insect olfactory sensilla. Symp. Zool. Soc. London *23*, 279–297.